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Variation in Mechanical Strength of Ferns in the Santa Monica and Santa Cruz Mountains

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Abstract

In recent years, experts in plant physiology have begun to explore the functional traits of ferns, especially in regards to their tissue-water relations. However, to our knowledge, no scientist had yet examined the relationship between fern biomechanics and physiology. We examined the mechanical properties of fern stipes (stems) and attempted to relate those properties to ecological and physiological traits. Based on our knowledge of fern anatomy, we hypothesized that stipe mechanical strength would not correlate with cavitation resistance as it does in seed-bearing plants.

This assertion that mechanical strength will not relate to cavitation resistance begs the question of what it does relate to. Therefore, we attempted to characterize the variation in the mechanical strength of fern species by examining the microclimate and ecological niche of each species.

Introduction

All vascular plants have vascular tissue containing, in part, conduits that transport water and minerals from the roots of a plant to its leaves. The two types of conduits in the xylem tissue are tracheids and vessels. Tracheids have non-perforate end walls through which the water must pass. On the other hand, vessels are composed of vessel elements that have perforate end walls, creating a hollow tube. Water moves upwards through the xylem due to the negative pressure created by the evaporate pull of water from the stomatal pores in the leaves. Difficulty arises in the case of low water supply, because the water continues to evaporate from the leaves, increasing the negative pressure on the water in the xylem. When the pressure exceeds a threshold, the water separates due to air seeding. This separation is also known as cavitation. This event is followed by an air bubble formation known as an air embolism, which blocks water transport. Embolisms in the conduits are difficult to repair under negative pressures in dehydrated tissues. Ferns have unique means for protection against cavitation, many of which are not completely understood (Pittermann 2011).

In seed-bearing plants, the mechanical support for the entire stem lies in the supporting fibers that surround these conduits. This mechanical support provides the plant with protection against cavitation (Jacobsen et al. 2005). Plant species with more mechanical support have been shown to be more cavitation resistant due to this fiber-strength protection (Jacobsen et al. 2005). However, current anatomical theory states that in ferns, the mechanical support for the stipe (stem) lies in the hypodermal sclerenchyma tissue just under the epidermis around the perimeter of the stipe, leaving the central xylem without any support tissue.

Given our current understanding of fern anatomy, it would be of utmost interest to compare the mechanical strength of several fern species. If indeed the mechanical support for the stipe lies solely around the perimeter and not within the xylem, there should be no difference in stipe mechanical strength among fern species that are more and less resistant to water stress. Therefore, we hypothesized that there would be no significant difference in the mechanical strength of the stipes of water-stress resistant and water-stress sensitive species of fern.

It should be noted that Jacobsen et al. (2005) used susceptibility to cavitation as a surrogate for resistance to water stress. In this study, we proposed to test water stress by means of the osmotic water potential at the turgor loss point ($\Psi_{II, TLP}$), percent soil moisture, and minimum seasonal water potential (Ψ_{min}). We also compared our two measures of cell wall elasticity (bulk modulus of elasticity and MOE) to justify our use of pressure-volume curves in analysis of fern stipes.

Finally, we took data to characterize the microclimate of each site, since variation in microclimate has been shown to correspond with differences in tissue-water relations (Gullo et al. 2010).

Hypothesis: There will be no significant difference in the mechanical strength of the stipes of water-stress resistant and water-stress sensitive species of fern.

Species Examined

Af – <i>Athyrium filix-femina</i>	Wf – <i>Woodwardia fimbriata</i>
Aa – <i>Adiantum aleuticum</i>	Ac – <i>Adiantum capillus-veneris</i>
Pm – <i>Polystichum munitum</i>	Pc – <i>Polypodium californicum</i>
Pg – <i>Polypodium glycyrrhiza</i>	Pn – <i>Pellaea andromedifolia</i>
Pq – <i>Pteridium aquilinum</i>	Pt – <i>Pentagramma triangularis</i>
Da – <i>Dryopteris arguta</i>	Aj – <i>Adiantum jordanii</i>

Materials and Methods

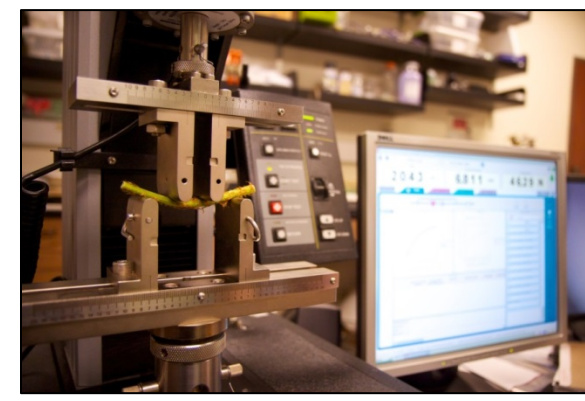


Fig. 1: Mechanical strength was measured with a four-point bending test on an Instron mechanical testing machine.

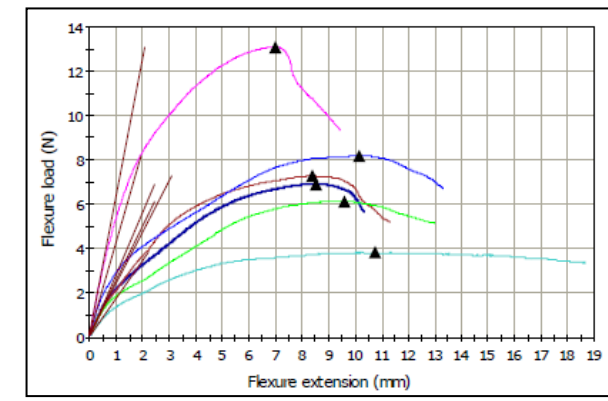


Fig. 2: Mechanical strength was measured in terms of Modulus of Elasticity (MOE) and Modulus of Rupture (MOR).



Fig. 3: Pressure-volume curves were generated using a Scholander-Hammel pressure chamber, following the methods of Saruwatari and Davis (1989).

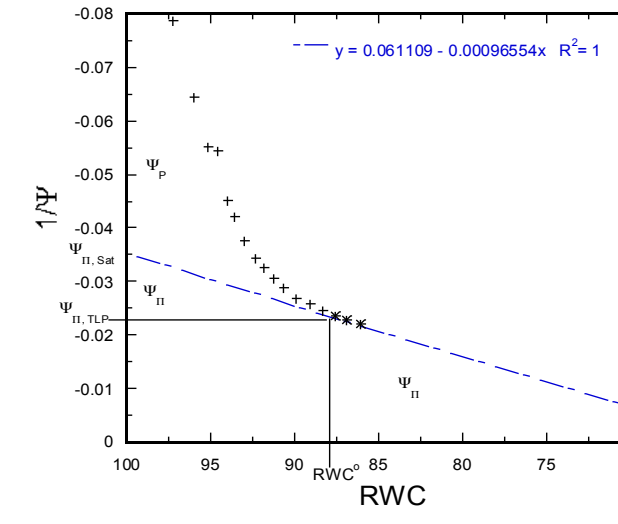


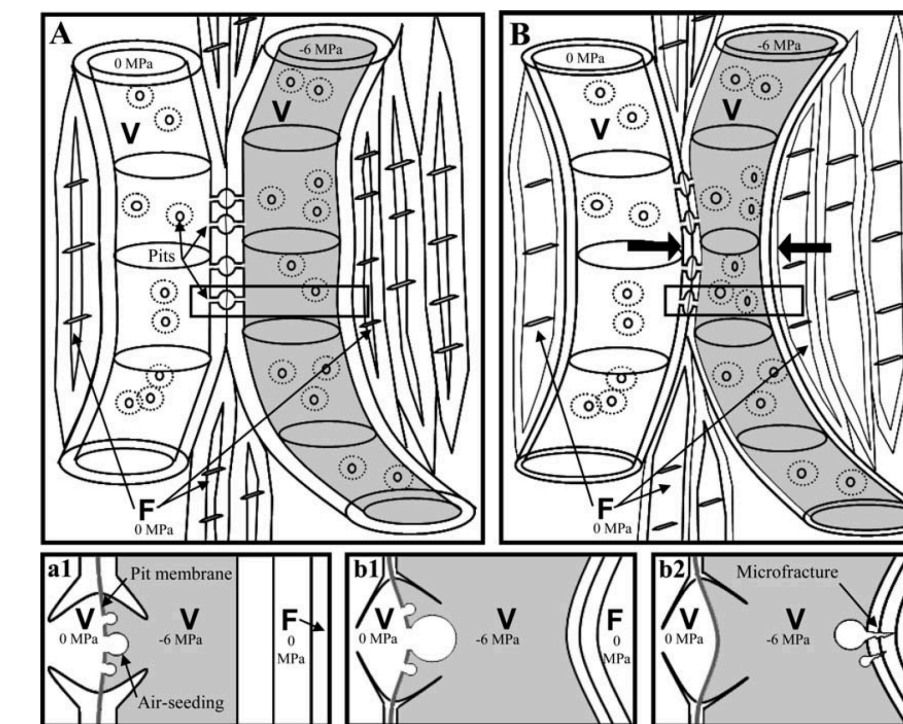
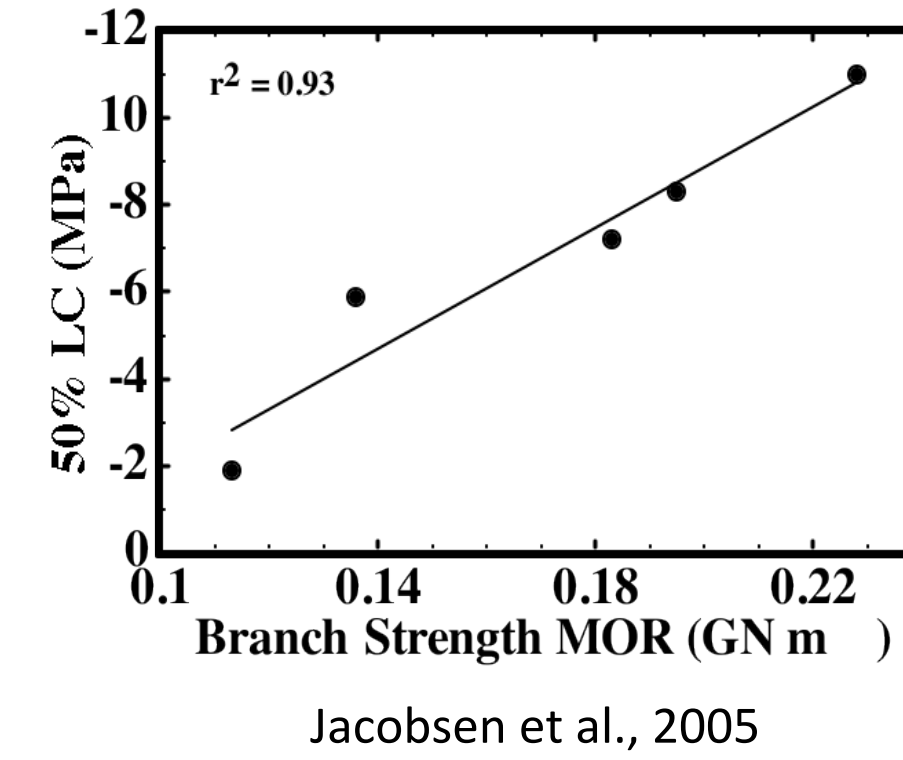
Fig. 4: Anatomical measurements were made using a light microscope, an ocular micrometer, and ImageJ software.

Fig. 5: Photosynthetically active radiation (PAR) was measured with a sun fleck ceptometer. Soil moisture was measured with a soil moisture meter. Air temperature, RH, dew point, and wind speed were determined using a Kestrel weather meter and leaf, soil, and air temperature adjacent leaves with an infrared radiometer.



Related Studies

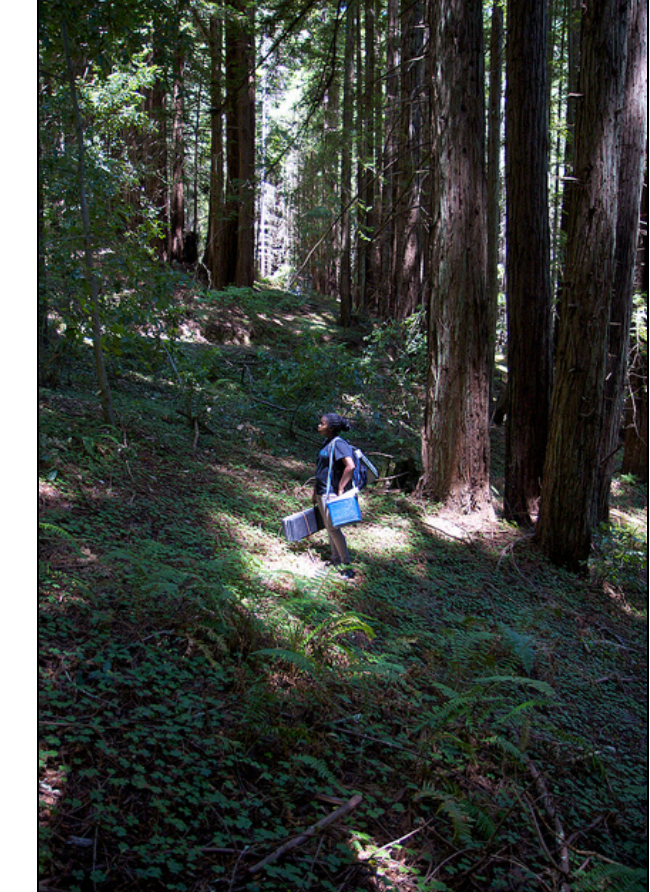
Previous studies of seed-bearing plants have shown a strong correlation between stem mechanical strength and cavitation resistance (50% LC). Jacobsen et al. (2005) attributed this correlation to the strong fibers embedded in the xylem of the stem. Since ferns do not have these fibers in the vascular tissue, we reasoned that there should be lack of such correlation.



Study Sites



Santa Monica Mountains: We sampled ferns growing among the chaparral species in a dry climate. We used fern species growing in three canyons.



Santa Cruz Mountains: We sampled ferns growing both in Henry Cowell Redwoods State Park and on the UC Santa Cruz campus. This site experiences about twice the annual rainfall as does our site in the Santa Monica Mountains.

Discussion

Our results are consistent with our original hypothesis that water-stress resistance in ferns does not relate to stipe mechanical strength. All three of the parameters that we tested did not appear to correlate with mechanical strength. Additionally, we correlated two measures of elasticity, which helped support our use of pressure-volume curves to assess the tissue-water relations. The strong positive correlation between bulk modulus of elasticity (obtained from the pressure-volume curve) and MOE (obtained from the four-point bending test) gave us confidence that we were accurately assessing the tissue-water relations of the stipes. We felt justified in omitting the two outliers in the correlation of bulk modulus of elasticity and MOE because of their unique lateral branching structure, which might create the need for greater mechanical strength.

Conclusions

- The osmotic water potential at the turgor loss point does not correlate with MOE.
- There does not appear to be correspondence between percent soil moisture and MOE.
- The minimum seasonal water potential does not correlate with MOE.
- Data obtained from pressure-volume curves of the end of the frond is a fair way to assess the tissue-water relations of the stipe.
- Therefore, there is no correlation between water-stress resistance and mechanical strength in ferns.

Literature Cited

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Acknowledgements

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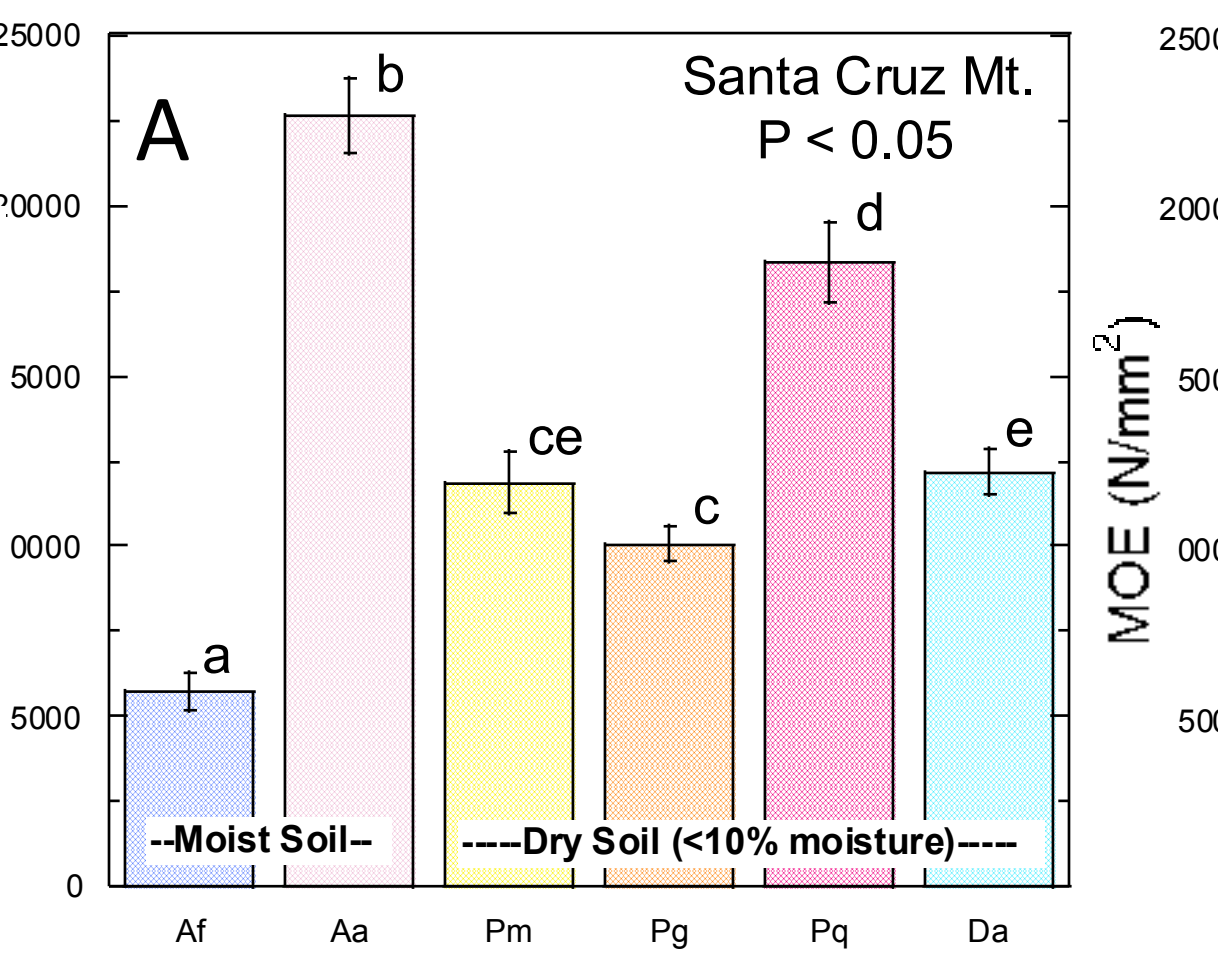
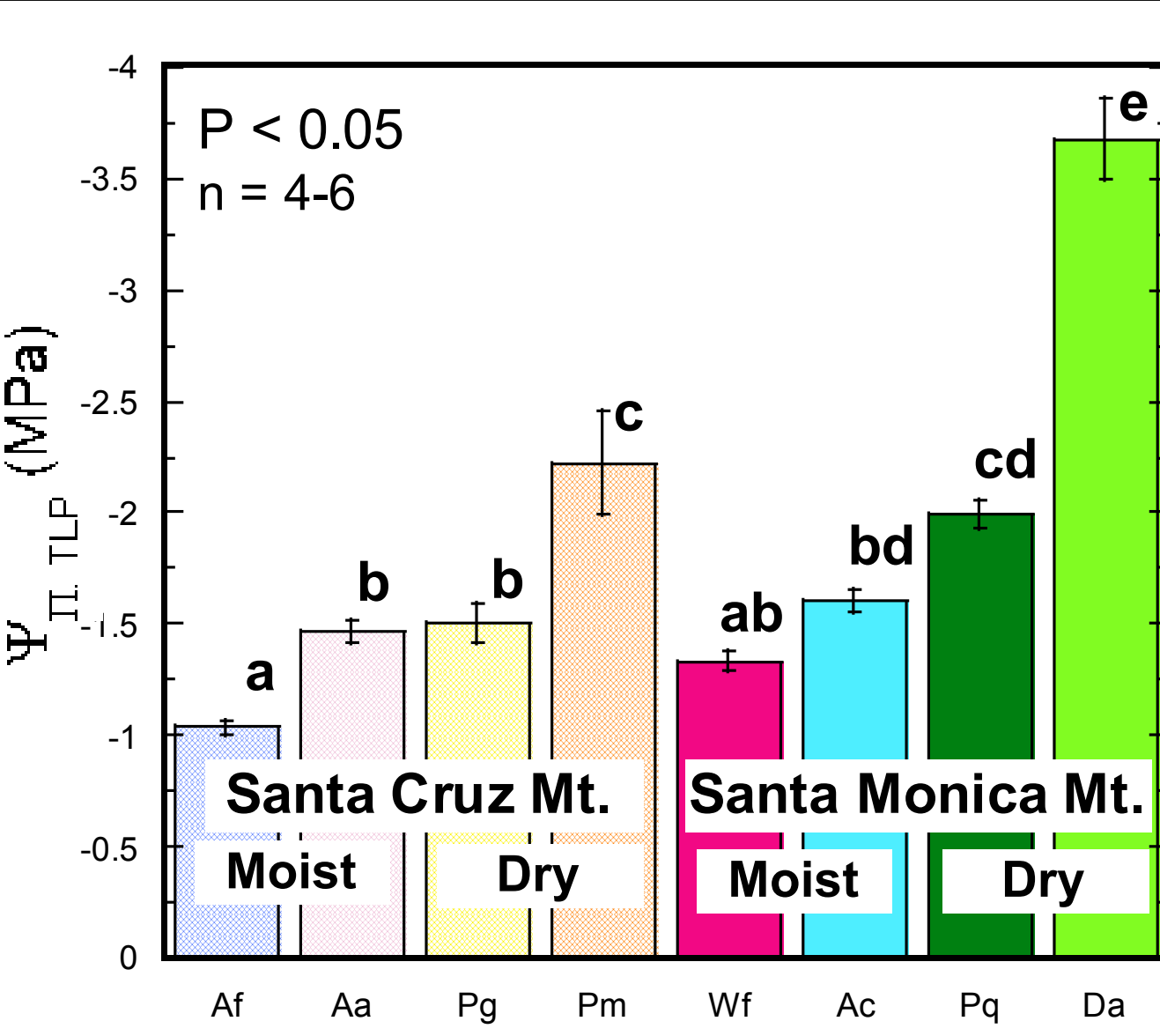


Fig. 8: Mechanical strength (MOE) of fern stipes compared among a) six species of the Santa Cruz Mountains and b) eight species of the Santa Monica Mountains by one-way ANOVA, followed by Fisher LSD Test. Different letters denote significant difference at $P < 0.05$. Bars represent ± 1 S.E., $n = 9-26$.

Results

Fig. 6: Osmotic water potential at turgor loss point ($\Psi_{II, TLP}$) of fern stipes compared among four species of the Santa Cruz Mountains and four species of the Santa Monica Mountains by one-way ANOVA, followed by Fisher LSD Test. Different letters denote significant difference at $P < 0.05$. Bars represent ± 1 S.E., $n = 4-6$. Moist soil is defined here as having >10% soil moisture and dry soil is defined as having <10% soil moisture.

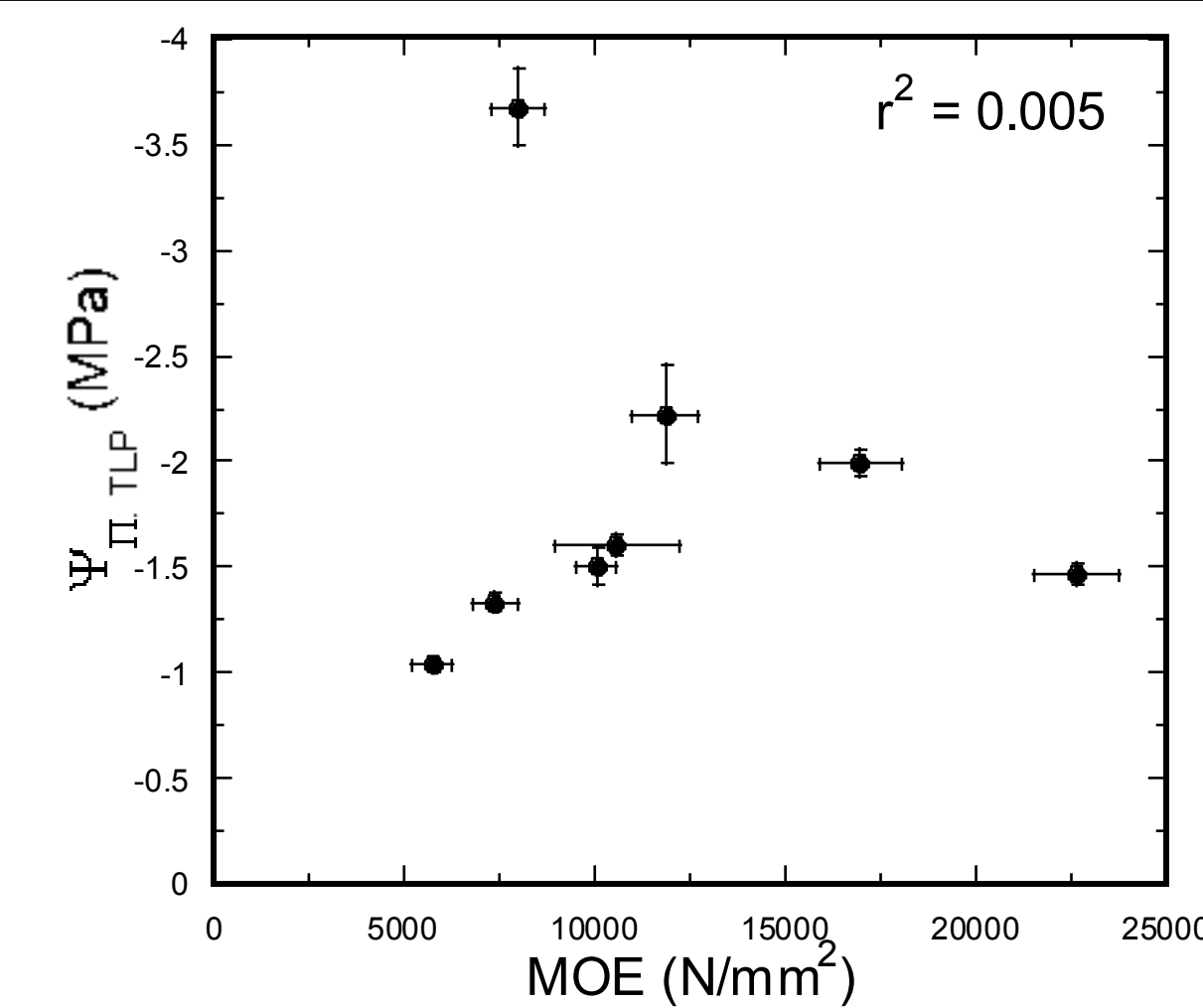


Fig. 7: Osmotic water potential at the turgor loss point ($\Psi_{II, TLP}$) versus MOE. Bars represent ± 1 S.E., $n = 4-6$.

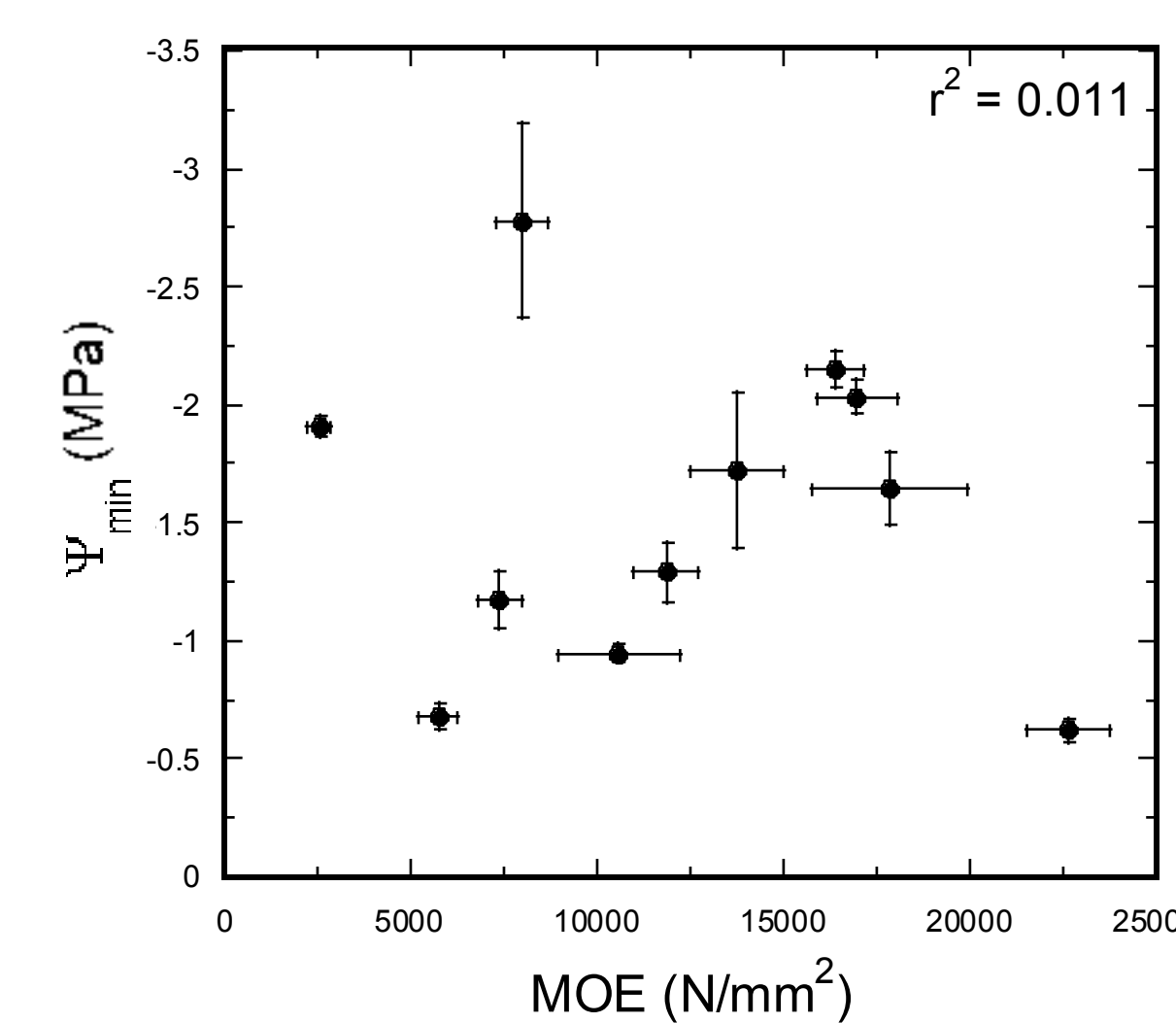


Fig. 9: Comparison of Ψ_{min} to MOE. Bars represent ± 1 S.E., $n = 3-13$.

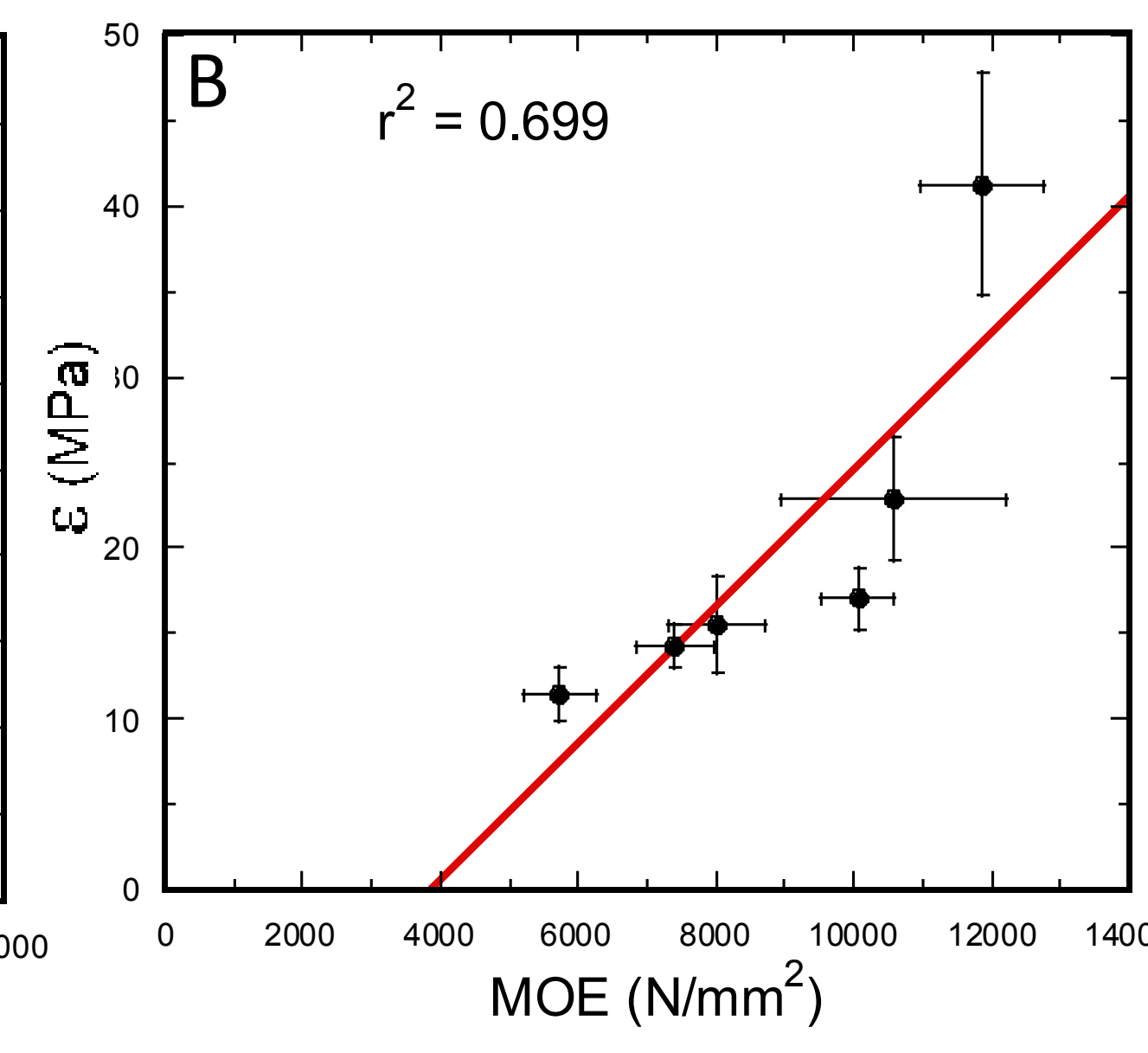
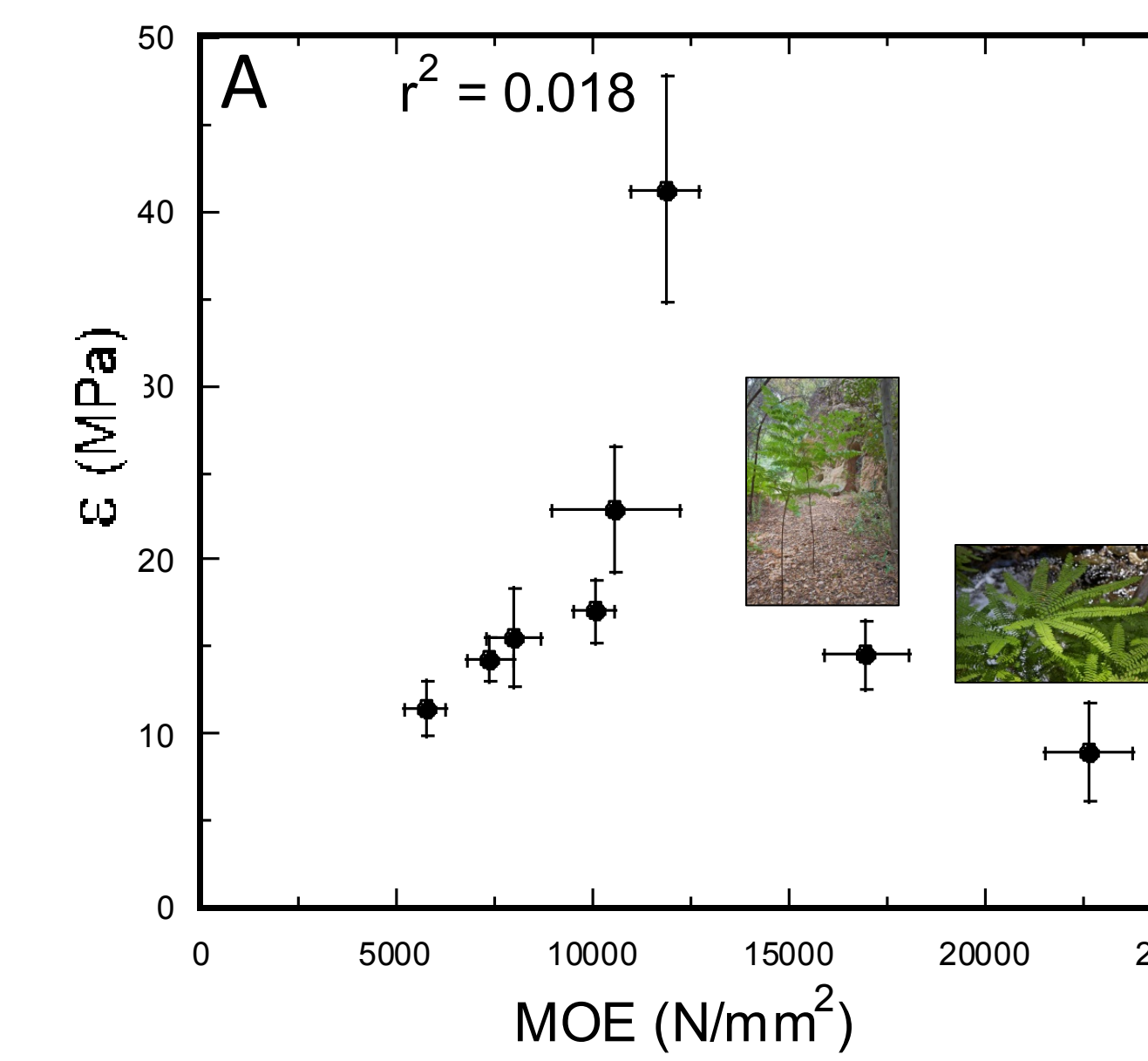


Fig. 10: a) Bulk modulus of elasticity (ϵ) versus MOE. Bars represent ± 1 S.E., $n = 4-26$. Pictures of *Pteridium aquilinum* and *Adiantum aleuticum* demonstrate unique lateral branching. Is it possible they require greater mechanical support? b) Bulk modulus of elasticity (ϵ) versus MOE after two outliers were omitted (Pq and Aa – both laterally branched species). Bars represent ± 1 S.E., $n = 4-26$.